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Spatial non-stationarity effect of determinants regulates variation in amphibian species richness

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ABSTRACT

Despite the variation in amphibian biodiversity being often explained through environmental variables, the effects of spatial non-stationarity factors are too-often ignored as significant geographic characteristics, especially at large scales. Here, using a spatial regression approach through a multiscale analysis, we explored the spatial heterogeneity and scale effects in the impacts of environments on amphibian species richness across China. We showed that the impacts of variables varied with regions, and the individual scales specific to each variable were negatively correlated with effect sizes. We then demonstrated that climate variables, followed by topography, showed a high explanatory power for species richness in most areas, while the effects of precipitation and temperature were characterized by high geographical heterogeneity. In addition, elevation was positively related to local species richness in most plains, while being a main negative variable to species richness in the western highlands. The analysis of geographic heterogeneity showed that the explanatory power of most variables declined with increasing elevation. Although anthropogenic impacts contributed less than climatic variables, they significantly increased the sensitivity of amphibian species to environmental variations. Finally, to measure the aggregation pattern of heterogeneous effects of variables on species richness, we used a neural network to identify ecoregions regulated by similar variables and determined the presence of four ecologically consistent regions. Our findings provide further evidence supporting spatially variables regulators of amphibian diversity.

1. Introduction

Species richness greatly varies between ecosystems, in close relation with environmental factors such as climate and topography. Specifically, species' diversity is regulated by spatiotemporal variables that can reflect complex characteristics, uniqueness and the extent of threats to biodiversity (Albrecht et al., 2021; Bonn et al., 2002; Seaborn et al., 2021). This environmental heterogeneity determines the spatial patterns of biodiversity, along with spatial variations in climatic and geographic elements, the diversity of natural conditions and resource availability (Fu et al., 2006; Mantyka-Pringle et al., 2013; Stein et al., 2014). Thus, geographic variation in variables associated with biodiversity largely explains the spatial aggregation of species richness.

Amphibians are currently the most threatened taxa of vertebrates globally (Ceballos et al., 2020; Stuart et al., 2004). Since before the 1970s, amphibian species have dramatically declined in numbers and they are now suffering from a global extinction crisis (Alford et al., 2001; Ceballos et al., 2015). As ectothermic animals, amphibians are more sensitive to environmental changes than other species (Nowakowski et al., 2017; Radchuk et al., 2019), and fluctuations in temperature and precipitation resulting from habitat degradation and climate change are significantly affecting their physiology (Chen et al., 2011). More than 40% of amphibian species worldwide are threatened by range reduction and habitat quality decline due to human activities, and even in areas

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with low human influence, amphibians are vulnerable to changes in environmental factors (Kiesecker, 2011; Lips et al., 2008). Therefore, in-depth analyses of amphibian diversity and dynamic mechanisms will guide regional ecological policies, support targeted ecological security, and help understand how species respond to environmental change.

At present, the variables explaining geographic variation in amphibian richness are challenging to generalize, and regional studies often vary considerably, especially regarding spatial responses to climate, topography, and human impacts. For instance, species richness along an elevational gradient is best characterized as a linear function of water availability (i.e., precipitation and drought conditions), and a non-linear function of energy availability (i.e., temperature, potential evapotranspiration and solar radiation) (Chettri and Acharya, 2020). In addition, reduced precipitation can lead to dramatic changes in amphibian biodiversity patterns, even potentially resulting in populations and species extinction (Ochoa-Ochoa et al., 2012). Amphibian species richness in East Asia follows a linear positive correlation with temperature and precipitation, but it is weakly correlated with net primary productivity (Zhao et al., 2006); in contrast, the effects of climatic variables on amphibian distribution are non-linear across the eastern Mediterranean coastal region (Kafash et al., 2018); and alternatively, temperature contributes more than precipitation to species richness in southeastern Brazil and semi-arid areas of North America (Esparza-Orozco et al., 2020; Rebouças et al., 2021). Thus, the mechanisms regulating the geographically variable responses to biodiversity at various scales are still unclear.

In addition, the linear and non-linear relationships mentioned above are affected by spatial heterogeneity and scale effects (Kerr and Packer, 1997; Nogués-Bravo et al., 2008). Linear effects of factors may become non-linear when the resolution of spatial sampling is improved, or the scale is increased (Qian et al., 2007). The mechanisms regulating richness patterns in amphibian species vary through different climatic zones, with heterothermic species from high latitudes being more susceptible to the physiological effects of climate change than tropical species; and with the prominence of factors varying across locations (Gerick et al., 2014). For example, the effect of climatic spatial heterogeneity on vertebrates may be higher in the Neotropical and Oriental realms, where biodiversity is high, than at some higher latitudes in the Palearctic (Pacifici et al., 2015). In contrast, the richness of amphibians is greatly regulated by elevation in some high-altitude areas where survival conditions become extreme (Chettri and Acharya, 2020; He et al., 2020). Thus, under the synergistic effects of multiple ecological processes, the impacts of environmental variables on amphibians are variable across landscapes, and also scale-dependent, which is defined as a spatially non-stationary relationship. As a result, the spatial non-stationarity is a non-negligible factor explaining spatial variation in amphibian diversity, and effectively reflects the specific responses of the clade to environmental changes in different areas (Buckley and Jetz, 2007).

Despite substantial efforts dedicated to illustrating the determinants of variation in biodiversity within specific areas, the understanding of spatially non-stationary relationships between amphibian species richness and multiple factors is still tenuous. Previous studies primarily relied on stationary analytical methods (Chi et al., 2021; Crawford et al., 2010; Paradis, 2018; Zhang et al., 2020), with a primary focus on the overall relation between species richness and community composition with environmental variables (Azevedo et al., 2021; Parris, 2004), including natural and anthropogenic variables (Ashrafzadeh et al., 2019; Gouveia et al., 2013; Green et al., 2019). However, the dependent structure and non-stationarity of spatial anisotropy will increase with the expansion of the research scope (Liu et al., 2021), and the assumption of stationarity in the effects of environmental variables on ecological pattern is unlikely to be applicable to large-scale studies.

Generalized linear models do not take into account the spatial variation between the response and explanatory variables, in which the relationships between variables are assumed to be constant across the space. The geographically weighted regression (GWR) model is an extension of ordinary linear regression models, which considers the spatial heterogeneity of influencing factors (Chien et al., 2020). It has been applied to analyze the spatial variation in the relationship between environmental factors and biodiversity (Roll et al., 2015; Ye et al., 2021). Although standard GWR can capture the spatial heterogeneity of ecological mechanisms, it assumes that different variables act at the same spatial scale. Excessive bandwidth increases the residual error of local model estimation, and fewer sampling points due to a small bandwidth increases the uncertainty of parameter estimation (Yu et al., 2020). MGWR is a spatial regression approach based on multi-scale analyses, which allows detecting the relationships at varying spatial scales (Dutta et al., 2021). MGWR offers novel insights into examining the spatial non-stationarity of ecological processes, and has been used in regional studies to investigate the sensitivity of vegetation to drought and local niche–genotype relationships of reptiles (Dong et al., 2023; Inman et al., 2019).

Thus, our study introduces MGWR to determine the prioritization of factors, and quantify the relationship between effect size and acting scale to reveal the impact of scale-dependent variables on biodiversity. We aim to explore how amphibian species richness varies in response to environments across China, and test how determinants regulate geographic pattern of species at various scales. Finally, we used a neural network approach to identify four regions and subregions affected by a unique combination of determinants. The analysis presented here provides a novel insight into the identification of explanatory factors of amphibian biodiversity and compares the ecological mechanisms in various regions. Our results are significant indicators for biodiversity conservation and ecological policy guidance.

2. Materials and methods

2.1. Study area

China hosts a significant regional biodiversity and a large number of endemic and threatened species (Luo et al., 2015). The climate gradient varies considerably: eastern China is characterized by a monsoon climate and western China has a temperate continental and alpine climate. Complex and diverse landforms such as high elevation plateaus and alluvial plains, clear boundaries between dry and wet areas, and rich vegetation types promote the diversity of amphibian habitats (Fig. 1).

2.2. Species data

The distribution data for 487 species of amphibians in this study was derived from the website of the International Union for Conservation of Nature (IUCN) Red List of Threatened Species (IUCN, 2021), including 413 species of Anura, 73 species of Caudata and 1 species of Gymnophiona. Data were spatial polygons of distribution that represent the known ranges of species. Species richness was calculated by counting the total number of species occurring in each grid cell. While the range of numerous species has been updated since the download in 23 September 2021, these updates are generally refinements in species range, with a resolution below that of the one used in our study, and thus not impacting our results.

In general, the distribution of amphibian species in China is regionally heterogeneous. Low latitudes with subtropical monsoon climates have a higher species richness (Pearson correlation between species richness and latitude = -0.62, $p < 0.01$), and few species distribute in the high elevations of the western region (Fig. 1). Species richness in central China follows the topographic pattern, with a higher richness around the Sichuan Basin than within the basin (Fig. 1). The greatest species richness is in Yunnan in southwest China, while the lowest richness is located in both the west and northwest. As a result, there is a significant spatial autocorrelation for pattern of species richness when exploring the spatial data (Moran's index = 0.848*).

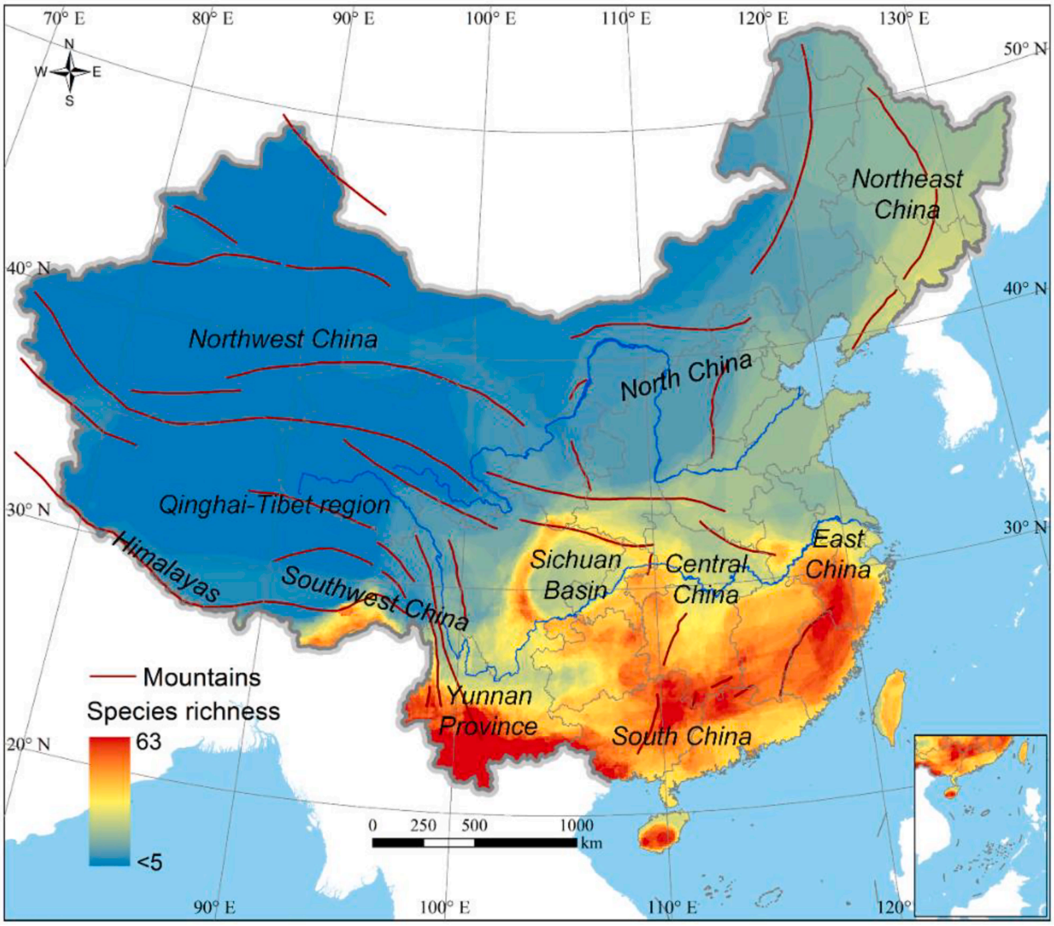

Fig. 1. Pattern of amphibian species richness in China. The color scale reflects the variation in the number of amphibian species.

2.3. Environmental data and covariates selection

The climate stability hypothesis holds that current climate conditions such as precipitation and temperature primarily determine species distribution and dispersion abilities (Dubos et al., 2020; Klopfer, 1959). Next, the productivity and ambient energy hypotheses indicates that amphibian biodiversity is closely related to solar radiation energy (Currie, 1991). In addition, the habitat heterogeneity hypothesis holds that topographic characteristics of the regional microenvironment directly or indirectly affect biodiversity patterns (Kerr et al., 2001). At present, the exploration of the spatial heterogeneity of amphibian species richness is limited, and there is no comprehensive understanding of the impacts of climate, topography and human activities, particularly in areas with high anthropogenic activities.

For the reasons stated above, eleven key variables were used for MGWR modeling. Among which, (1) five climate factors: average annual precipitation, precipitation seasonality, annual mean temperature, mean diurnal range, and surface solar radiation; (2) topographic and geomorphological factors: elevation, slope, relief amplitude, drainage density and normalized difference vegetation index (NDVI); and finally (3) we used human footprint index (HFI) to represent the intensity of human activity. HFI ranged from 0 to 50 and was typically divided into low pressure (0–2), moderate pressure (3–5), and high pressure (>5) (Venter et al., 2016b).

We derived the climatic data (30 arc second) from the WorldClim database (https://www.worldclim.org), including all 19 bioclimatic variables (Fick and Hijmans, 2017). We also obtained a high spatial resolution (10 km) surface solar radiation dataset from the National Tibetan Plateau Science Data Centre (Feng and Wang, 2021). Then, we derived the elevation data (30 m) from the ASTER Global Digital Elevation Model Version 2 (ASTER GDEM2) and calculated the relief amplitude by subtracting the minimum to the maximum elevation within a 5 km^2 window. The drainage density was generated by the line density estimation method in ArcGIS 10.2, based on the line feature data of the drainage systems, which we derived from the National Catalogue Service for Geographic Information (https://www.webmap.cn). The normalized difference vegetation index data (10 km) was available from the National Earth System Science Data Center (https://www.geodata.cn). We also used the human footprint index (Version 2) (1 km) as it is a comprehensive indicator to quantify the pressure of human activities on the environment (Venter et al., 2016a), and it is available from the Socioeconomic Data and Applications Center (SEDAC, https://sedac.ciesin.columbia.edu). The dataset was composed of eight variables that can effectively reflect the human impacts on biodiversity and ecological landscape (Correa Ayram et al., 2017). All data were converted to grids with a cell size of 60 × 60 km. The variance inflation factor (VIF) of all variables was <7.5 (Table S1), and there was no redundancy among variables.

2.4. Multiscale geographically weighted regression

The multiscale geographically weighted regression (MGWR) model can select the appropriate bandwidth according to each variable's spatial characteristics and autocorrelation, and also find the optimal spatial sampling range of local stationary regression (Li and Fotheringham, 2020). The MGWR considers the scale variability of each explanatory variable in the fitting process, meaning that each spatial object has a specific spatial weight matrix for the corresponding variable

(Fotheringham et al., 2017), thus effectively measuring the spatial scale-dependency of the variable. The MGWR model expression is as

$$y_i = \beta_{bw0}(u_i, v_i) + \sum_{j=1}^{m} \beta_{bwj}(u_i, v_i)x_{ij} + \varepsilon_i \quad (1)$$

Where, (*ui*, *vi*) is the spatial location of point *i*; x_{ij} and ε_i represent the *j*th explanatory variable and random error at location *i*, respectively; β_{bw0} is a constant term; *bwj* is the bandwidth used to calculate the regression coefficient of the *j*th explanatory variable; β_{bwj} (u_i, v_i) is the regression coefficient of the *j*th explanatory variable at the spatial location *i*. The estimated value of the MGWR coefficient varies with the spatial weight matrix, and it is computed such as in equation:

$$\beta(u_i, v_i) = \left(X^T W(u_i, v_i)X\right)^{-1} X^T W(u_i, v_i)y \quad (2)$$

Where β (u_i, v_i) is the unbiased estimation of model coefficients; *X* is the explanatory variable matrix; *y* is the dependent variable; *W* (u_i, v_i) is the spatial weight matrix. Here, the Gaussian kernel function is used as the weight function for calibrating model. Bandwidth is a function to describe the weight and distance, which were optimized using the Corrected Akaike Information Criterion (AICc). We implemented the MGWR model in the MGWR 2.2 software (https://sgsup.asu.edu/sparc/mgwr).

2.5. Self-organizing feature mapping network

The self-organizing feature map (SOM) is a non-linear classifier based on artificial neural networks, with the advantages of maintaining variable topology, high fault tolerance, and strong adaptability, which is widely used in studies such as ecological functional zoning (Mao et al., 2019; Mostafa, 2010). SOM adjusts the weights of the initial network through constant competition between nodes, eventually bringing nodes with similar features closer (Kohonen, 1982), therefore achieving better clustering results while keeping the topological structure of the variables unchanged.

Ecologically consistent regions are identified using SOM, where the effect sizes of the variables (outputs of coefficient estimate by MGWR) within each grid cell are considered as feature values for the model inputs. Grid cells with similar characteristics are aggregated into the same cluster group, which means that grid cells with similar regression coefficients of variables are classified as the same cluster and each variable has a similar effect size on species richness in any grid cell within each subregion. We performed the SOM analysis using the kohonen R package (Wehrens and Buydens, 2007). We assigned geographic coordinates to the clustering results. Changing the number of classes significantly affected the clustering results, thus the optimal number of clusters was calculated by the Calinski-Harabasz (CH) index.

2.6. Statistical analyses

We analyzed the drivers of amphibian species richness in China following three aspects: climate, topography, and human activity. Considering the spatiotemporal complexity of the model and the characteristics of species distribution data, we conducted the modelling at a 60 × 60 km grid-cell resolution. The eleven variables used in the modeling were selected when in absence of multicollinearity and based on their explanatory strength in model. We aimed to reduce the number of variables while incorporating representative primary indicators. We carried a cluster analysis on variables selected to test the rationality of each selected variable involved in the modeling, which were performed using the k-means R package (Hartigan and Wong, 1979). We found that the distribution of the classification had a certain coupling with the Chinese ecosystem type zoning (contingency coefficient = 0.807; Figure S3), suggesting that these eleven variables are well represented. We then used an ordinary least square (OLS) regression and geostatistical indicators to detect whether there is a spatially non-stationary relationship between species richness and environmental variables. MGWR was adopted to explore the spatial heterogeneity and scale dependence in the effects of variables. Finally, a neural network clustering approach was used to analyze the ecologically consistent regions with similar determinants.

3. Results

3.1. Occurrence of spatially non-stationary relationships between richness and factors

The OLS results (at 0.01 significance level) suggested that precipitation and temperature were the variables with the strongest overall effect size, followed by human footprint index, normalized difference vegetation index and topography (Table S1). The adjusted R^2 for this general linear model is 83.1%, indicating that a percentage of the variation in species richness can be explained by independent variables in China.

From the spatial statistical tests, we found that significant spatial non-stationarity existed in the relationship between covariates and species richness. The Jarque-Bera (JB) statistic indicated that the residuals of the model were not normally distributed ($p < 0.01$) and showed areas where richness was either overestimated or underestimated (Fig. S3a), with significant spatial autocorrelation (*Moran's I* = 0.721, $p < 0.01$). In addition, the Anselin Local Moran's I results showed a spatial clustering of residuals across areas (Fig. S3b). The distribution of residuals showed a similar aggregation pattern for species richness, as the overpredictions of OLS tended to occur in areas with the highest species richness, around which were the areas with underpredictions (Fig. 1 and Fig. S3b). If the effects of the variables involved had been spatially stationary, the error between the predicted and actual values of richness would not have differed significantly at any geographic location. However, the Koenker (BP) statistic used to detect heteroskedasticity in the model passed the significance test (*BP* = 612.37, $p < 0.01$), indicating that the relationship between variables and species richness varied by geographic location. Thus, the effects of variables were inconsistent across our study area and should be analyzed for spatial heterogeneity.

3.2. Geographic variations in the impact of variables

The MGWR model results showed that the response intensity and direction of amphibian species richness to climatic variables varied considerably across regions (Fig. 2, Table 1). A positive relationship indicates that the amphibian species richness tends to increase as the specific covariate increases, while a negative relationship shows an opposite trend. Specifically, annual precipitation was the main factor positively affecting species richness, where positive areas of regression coefficient accounted for 98.7% within the whole country, and most estimates were relatively high except in westernmost and northernmost China (Fig. 2a, Table 1). The direct effect of precipitation as well as the annual mean temperature showed a greater contribution in Southwest China. The annual mean temperature had a weak explanatory effect on species richness in western and northern areas, but a highest negative effect within the basin of Central China (Fig. 2c). Mean diurnal range showed decreasing negative effects from the south towards the northeast (Fig. 2d). The effects of surface solar radiation were negative everywhere, with the highest values mainly distributed at lower latitudes (Fig. 2e).

The effects of the topographic factors varied spatially, likely in relation with altitude. Elevation had a significant negative effect on amphibian richness in the west (Fig. 2g), especially on the plateaus, and a positive effect in eastern China (primarily plains). The exception to the spatial variations was for slope, with mainly non-significant differences across the whole area (Fig. 2h). The regression coefficient estimates of relief amplitude were primarily negative in the east and north, and they

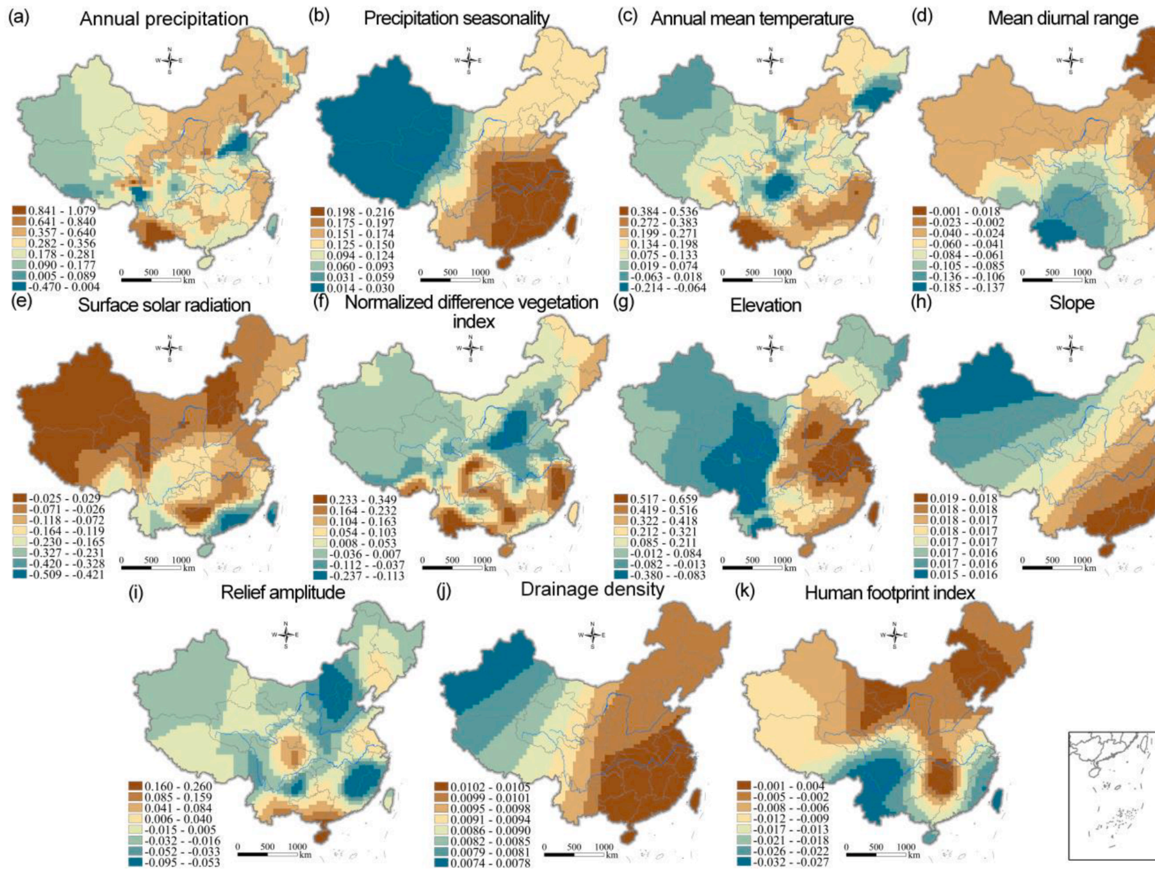

Fig. 2. Spatial variation of regression coefficient estimates for the MGWR model. Geographic distribution of local coefficient estimates of annual precipitation (a), precipitation seasonality (b), annual mean temperature (c), mean diurnal range (d), surface solar radiation (e), normalized difference vegetation index (f), elevation (g), slope (h), relief amplitude (i), drainage density (j) and human footprint index (k).

Table 1
Summary statistics for the MGWR model. Mean is the average value of the coefficient estimates, Min the minimum value, and Max the maximum value. The MGWR model is fitted at the local scale with a specific bandwidth for each variable and the bandwidth reflects the variations in the action scales among variables. The proportion of positive area represents the grid cells with positive MGWR estimated coefficients as a percentage for the study area. Asterisk indicates the mean significance level in areas with species present (* $p < 0.01$).

Variable	Coefficient estimate					Bandwidth (km)	Proportion of positive area (%)
	Mean	STD	Min	Median	Max		
Annual precipitation	0.306 *	0.174	−0.470	0.277	1.079	43	98.7
Precipitation seasonality	0.107 *	0.076	0.014	0.137	0.216	448	1.0
Annual mean temperature	0.118 *	0.108	−0.214	0.105	0.536	51	89.7
Mean diurnal range	−0.048 *	0.037	−0.185	−0.035	0.018	240	7.0
Elevation	0.126 *	0.231	−0.380	0.008	0.659	60	52.0
Slope	0.017 *	0.001	0.015	0.017	0.018	2608	100.0
Relief amplitude	−0.013 *	0.035	−0.095	−0.019	0.260	137	17.3
Drainage density	0.009 *	0.001	0.007	0.010	0.010	2608	100.0
Normalized difference vegetation index	0.029 *	0.085	−0.237	0.003	0.349	51	52.0
Surface solar radiation	−0.071 *	0.083	−0.509	−0.046	0.029	91	14.1
Human footprint index	−0.010 *	0.008	−0.032	−0.008	0.004	518	3.1
Intercept	−0.002 *	0.609	−0.689	−0.120	1.595	43	33.3

were not significant in other areas (Fig. 2i). The overall effects of drainage density on species richness were positive, presenting a spatial distribution characteristic of "low west and high east", and displayed a stripped distribution (Fig. 2j). By overlaying the maps of species richness and coefficient estimates, we found that areas with the most significant effects of normalized difference vegetation index were spatially congruent with species aggregation areas, thus mainly affecting areas with high species richness (Fig. 2f and Fig. 1).

In most areas, the local effects of the human footprint index were negative (Fig. 2k). The area with the largest negative coefficients was the southwest, where the pressure on amphibians caused by human activities was the highest. The peak values of coefficient estimates (positive or negative) for other variables increased significantly when the human footprint index was at the highest levels, indicating that the sensitivity of amphibians to environmental changes was significantly driven by human activities (Fig. 3). The negative effects of the mean diurnal range and surface solar radiation increased with the human footprint index (Fig. 3), and then reached a negative peak when the human footprint index > 30. The coefficients of relief amplitude and normalized difference vegetation index alternated between positive and

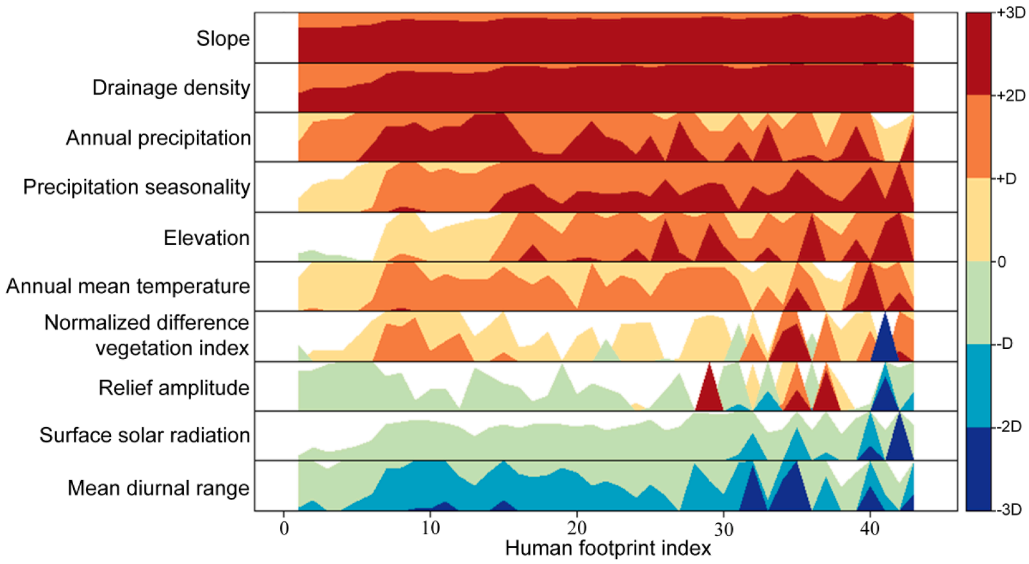

Fig. 3. Band superposition representative of the effects of covariates in relation with the human footprint index. The horizontal and vertical axes represent the human footprint index and coefficient estimates of other covariates in the MGWR model, respectively. For ease of display, the positive and negative ranges of the coefficient values for each variable are divided into six equal segments, labeled from −3D to 3D, where the D denotes the interval of three equal parts of positive values and -D represents that of negative values. The color band from yellow to red represents the increase in the positive effect of a variable, and the light blue to dark blue indicates the gradual increase in the negative effect of the variable. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

negative values, and the intensity of their effects showed multiple peaks at human footprint index > 27. We also found that the effects of these two variables were positive at low indices of human footprint index, but both abruptly showed a short-term high negative effect when the human footprint index > 40 (Fig. 3). In addition, the effects of slope and drainage density showed a steady trend across the landscape, suggesting that the explanatory power of these two variables for species richness was constant.

3.3. Geographic distribution of dominant variables

To understand the geographical distribution of the determinants in explaining species richness, we separately determined the factors with the highest contribution of positive and negative effects for each grid cell. Among the variables with positive effects (Fig. 4a), annual precipitation best explained the heterogeneity of amphibian species richness in western, southwestern, and northeastern China. Elevation best explained the amphibian richness in the eastern plains. In addition, some other variables had a high explanatory power of species richness (annual mean temperature, precipitation seasonality and normalized difference vegetation index), but their effect was restricted to small spatial ranges, and mainly distributed in the eastern Qinghai-Tibetan Plateau.

On the other hand, the analysis determining the negative contribution of variables (Fig. 4b) showed that species richness of western China was best explained by mean diurnal range and elevation, with a high explanatory power for the normalized difference in vegetation index and Annual mean temperature in some scattered areas. Mean diurnal range showed high contributions of highlands within western China and the plains in South China. Surface solar radiation was the dominant explanatory variables with negative effects in central and northeast China, and it was more strongly linked to species richness in the plains than on plateaus. Among the topographic factors, relief amplitude significantly affected amphibian species richness in the northern areas, while slope did not contribute significantly to species richness when compared to other variables.

3.4. Spatial scale-dependent characteristics of effects in variables

The scale dependence varied significantly among the types of

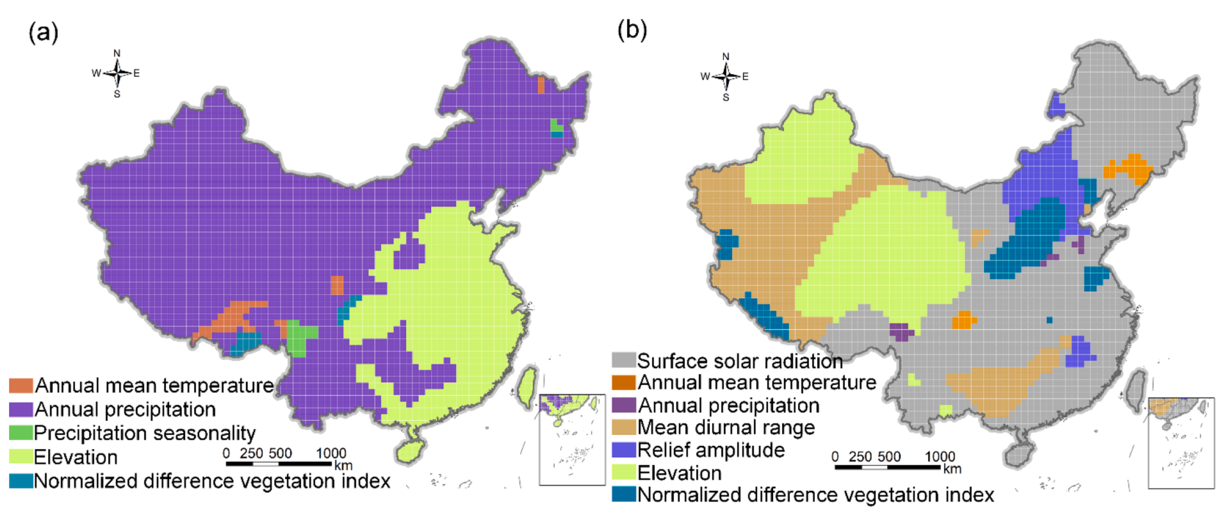

Fig. 4. Geographic distribution of variables with the main contribution to amphibian species richness. (a) Determinants with positive effects; (b) Determinants with negative effects. The color scale indicates the variable with the highest contribution within a given grid cell. The contribution of a variable to the species richness for a specific grid cell was evaluated by calculating the product of the coefficient estimate and the corresponding variable as a percentage of the dependent variable. The contribution of drainage density, slope and human footprint index were weaker than other variables for all cells and thus they are not shown on the figure.

variables, and most autocorrelations of residuals were explained by local regression intercepts with the specific bandwidths (Table 1). Smaller bandwidths indicated higher spatial heterogeneity in the effects of variables. Overall, the regression bandwidths of variables were negatively correlated with the effect sizes, and the fitted curve of effect size displayed a near exponential decay with bandwidth (Fig. 5). This pattern suggests that the stronger the effect intensity, the stronger the spatial non-stationarity relationship with amphibian species richness. The variables with the highest spatial heterogeneity were annual precipitation, annual mean temperature, normalized difference vegetation index and elevation, with corresponding bandwidths all<60 km (Table 1). Furthermore, slope and drainage density had the same effect scale, corresponding to the greatest bandwidth (bandwidth = 2608 km; Table 1), and tended to fall into a stationary relationship with species richness. These results indicate a weak geographic variation and a trend of effect toward stability. Other variables were acting locally as the geographic scales were around the median of bandwidths (MGWR bandwidths ranging from 90 to 520 km).

3.5. Ecologically consistent region with similar determinants

To analyze areas similarly affected by variables, we aggregated grid cells similarly affected by the variables regulating species richness, resulting in the division of the study area into four distinct regions (Fig. 6a). The variation in amphibian species richness in each subregion was regulated by different variables, which were closely related to the local environment. Specifically, annual precipitation was significantly explanatory for species richness within the Qinghai-Tibet and west desert region while the effects of the other variables were negligible (Fig. 6b). Elevation was particularly important to determine the species richness in the Central and northern region (Fig. 6b). The climate and geographic conditions in Yunnan were suitable for the highest amphibian biodiversity, with an average aggregation of 25 species within 60 km^2, and the richness was best explained by precipitation, temperature, surface solar radiation and the normalized difference vegetation index (Fig. 6b, Table S2). Species richness in the "southwest mountains and the southern region" was mainly affected by precipitation and elevation, followed by temperature as the boundary of this subregion was distributed along a mountain range (Fig. 6). In addition, by overlapping the regions we identified differences in local species richness. We found the transition zones between ecologically consistent subregions to be consistent with the aggregation pattern of species, and there were significant differences in the number of species on either side of the interregional boundaries (Fig. S4). For instance, the richness was concentrated on the southern side of the boundary between the Central and northern region (region II) and the Southwest mountains and southern region (region IV). This concentration of species richness in the south was largely explained by climatic factors, whereas species richness on the northern side were largely affected by topography (e.g., elevation).

4. Discussion

Our study provides a comprehensive analysis in terms of climate, topography, and human impacts to test the spatial non-stationary relationship between amphibian species richness and environmental variables. Our results suggest that apart from the generally high importance of the role of climate in eastern China, the importance of variables mediating amphibian species richness showed substantial variation across study area. Specifically, we demonstrate that elevation has a high impact on species richness at altitudes < 2000 m (Fig. 4 and Fig. S5), while precipitation and temperature were also substantial but rapidly decreasing with the increase in altitude (Fig. S6a). This is in line with the literature, as species richness is largely mediated by annual precipitation and annual mean temperature at the global scale (Brown, 2014; Chen et al., 2011; Qian et al., 2007). Thus, the negative effect of the elevation is to some extent reflected by the few amphibian species that can adapt to the climate of high elevation plateaus, such as *Nanorana parkeri* (Fei

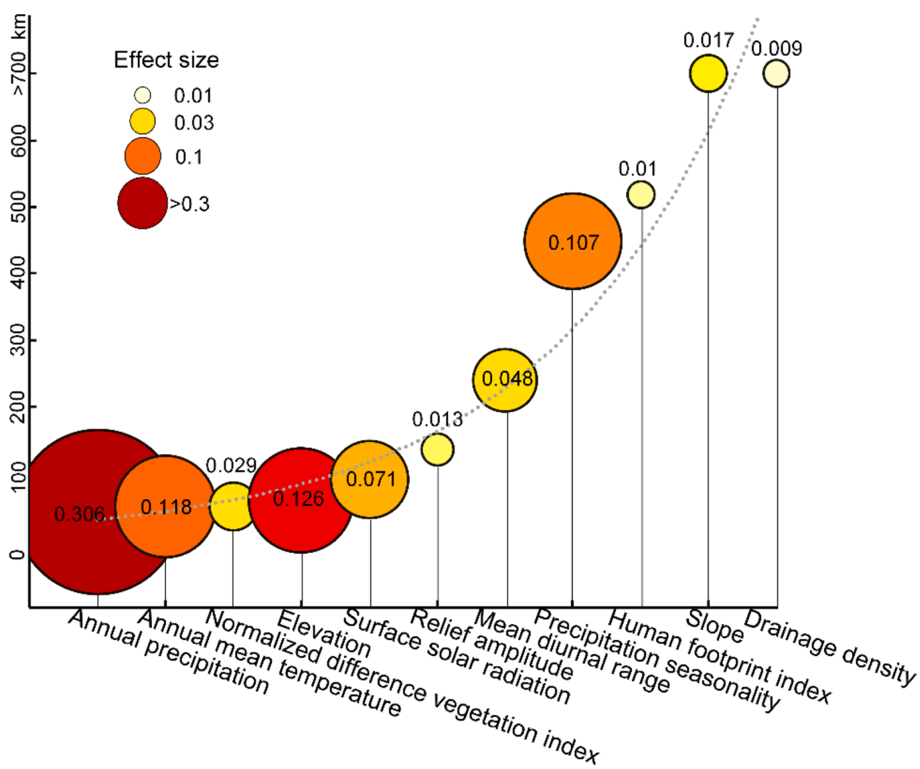

Fig. 5. The relationship between effect sizes and bandwidths. An individual bandwidth was determined for each variable by the MGWR model. The points in the coordinate system were given contrasting colors and radii to highlight the effects size of each variable (i.e., the absolute value of average coefficient estimates). The length of the vertical line from the center of each circle to the horizontal axis represents the bandwidth value (Y-axis).

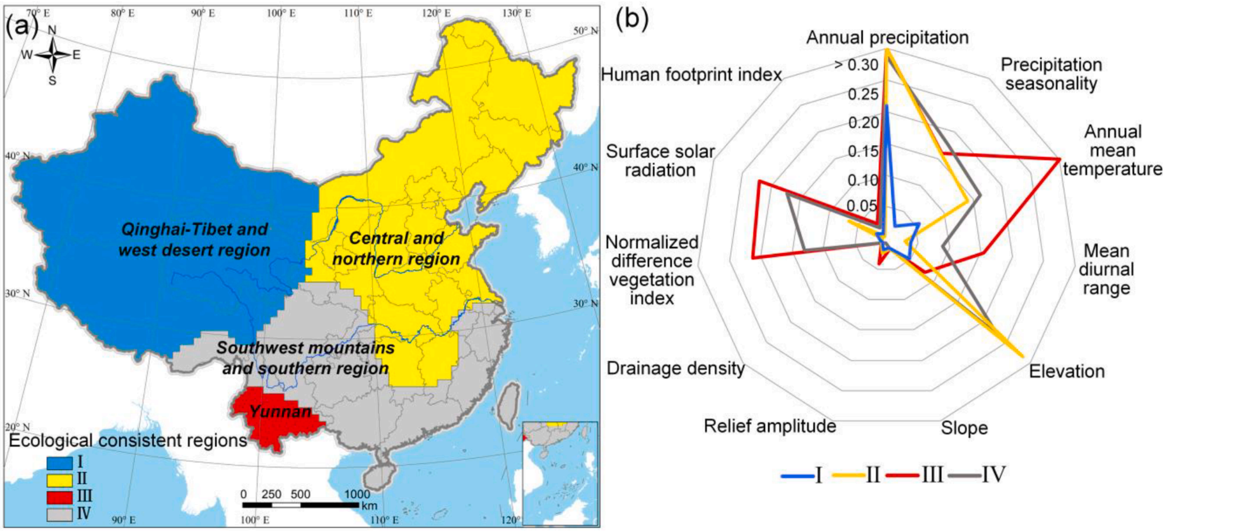

Fig. 6. Ecologically consistent regions identified using SOM. (a) The four subregions: the Qinghai-Tibet and west desert region (I), the central and northern regions (II), Yunnan (III) and the southwest mountains and southern regions (IV). (b) The average effect (absolute) of variable involved within each subregion. The grid cells across the areas were divided into several continuous subregions based on the matrix of MGWR coefficient estimates, indicating the combination of one or more variables that best explained the variation in species richness was similar at any location within a subregion.

et al., 2004a) and *Scutiger nyingchiensis* (Fei et al., 2004b) on the Tibetan Plateau. In addition, amphibians mainly occur in areas with stable temperatures (mean diurnal range < 11℃) because large diurnal temperature variations are not conducive to thermoregulation (Miller et al., 2018). Finally, increases in temperature exacerbated the suppressive effects of surface solar radiation on species diversity. Specifically, the relationship between spatial variation in temperature and regression estimates showed that the surface solar radiation had a higher negative effect on high-temperature areas compared to low-temperature areas, and the effect size increased sharply when the temperature was greater than 12 °C (Fig. S6b).

Although the effects of some variables were not significant in most areas (e.g., human influence index), the variation in the importance of these variables related to the scale of the studies and the impact of these variables are likely mitigated by the interaction with other processes, and thus should not be ignored. In addition, most variables showed generally high effects on species richness in areas of high human disturbance (Fig. 3), in relation with a risk of reduction in species richness. We also showed that species richness peaked in areas with a certain degree of human disturbance (human footprint index between 5 and 10; Fig. S7), in agreement with the intermediate disturbance hypothesis (Mayor et al., 2012). The negative impact of anthropogenic activities is likely due to the fact that humans and amphibians share the same habitat in areas with suitable environments. Finally, we demonstrated that relief amplitude and normalized difference vegetation index were negatively correlated with species richness when the human footprint index was high (HFI > 40, Fig. 3), while being positively correlated in other areas, indicating that human activity might alter the positive or negative impacts of variables depending on the species community and other correlated variables. Thus, our results do not support findings showing that species occurring in regions with less historical anthropogenic disturbance are more susceptible to environment changes (Ramírez-Delgado et al., 2022). Indeed, human activities have a lower effect on amphibian species diversity than environment factors when studied at a large geographic scale (Howard et al., 2020; Lu et al., 2020), while anthropogenic impacts have a significantly negative effect on amphibian biodiversity within small geographic areas (Ficetola and De Bernardi, 2004; Hamer et al., 2021). Our work provides evidence on why it is not ecologically meaningful to reach a geographically uniform conclusion in term of variables influencing amphibian species diversity, especially in view of the variation in species richness as a result of multiples factors operating at varying spatial scales and areas.

The analysis of scale effects suggests that the factors with a higher spatial heterogeneity are more effective in explaining the variation in amphibian species richness. For example, the significant effects of climatic variables on richness within small bandwidths; and the topographic factors, mainly affected species richness pattern at the macroscopic scales, especially slope and drainage density become stationary effects that can be explained by overall regression (Table 1). In the MGWR model, most variables operated at a local scale, and the effect size increased with decreasing bandwidth (Fig. 5). These findings capture a scale-dependent pattern specific to amphibian responses to the environment, and further demonstrate that the effective scale, as an important factor influencing the relationship between environmental variables and biodiversity, is differing considerably between variables in explaining species richness (Zhang et al., 2011).

The pattern of species richness showed a spatial characteristic varying with the heterogeneity of elevation. The largest number of species occurred between 500 and 2000 m, as predicted by vertical patterns of biodiversity (McCain, 2010; Rahbek, 1995). Elevation is the variable that best explains the negative variation in species richness in most highlands, while it becomes the most explanatory positive variable in the eastern plains (elevation < 1000 m; Fig. 2g and Fig. 4). This dichotomic effect provides evidence supporting vertical gradients in amphibian species richness. Moreover, the largest difference in species numbers occurred at the margins of Sichuan basin, the Himalayas and the mountains in southern China (Fig. S4). This spatial relationship between species gradients and topography is likely linked to geographic isolation limiting faunal dispersals (Goldberg and Lande, 2007; Hazzi et al., 2018). It is worth noting that although the species richness is low in the western China, the total number of species in Xinjiang and Qinghai-Tibet region is about 116 (about 23.8% of the total number of species). This suggests that amphibian species are not rare in western China, but with less overlapping distribution and thus less interspecific competition.

Further, our results show that in areas with the highest number of amphibian species, the species richness is regulated by integrative multivariate factors. Amphibians are mainly concentrated in landscapes with high vegetation cover, especially in Yunnan, where the normalized difference vegetation index and annual precipitation have significant regulatory effects on species richness (Fig. 2a and f). Species richness is promoted by both normalized difference in vegetation index and annual mean temperature in southern and eastern China (where the species richness > 28; Fig. 2c and f). Generally, complex habitats support more ecological niches due to the high environmental heterogeneity, and thus they are capable of hosting more species. These results are in agreement with the ambient energy hypothesis, which argues that increased environmental energy and water leads to higher net primary productivity, thus supporting a higher diversity or biomass (Evans et al., 2006). Even in both dry and wet areas with few species, variations in species richness are significantly affected by both precipitation and precipitation seasonality (Figure S8), reflecting the uniqueness of amphibian's water requirements (Zheng et al., 2021).

Here we applied a cluster analysis to identify the regions with variables having similar effects on species richness. The four regions we identified reflect the macro-regional pattern of amphibian species richness in response to environmental variables. We found the regions to be ecologically consistent and partially related to the topography and climate, despite this relation being area specific. The boundaries of the subregions almost coincide with topographical barriers, such as the highlands around the Sichuan Basin, the mountains in southern region and the western Tibetan Plateau (Figure S9). In addition, the junction of the different climatic zones showed a strong geographic congruence with the intersection of the subregions (Figure S10). These alignments suggest that the role of factors regulating amphibian diversity in different but ecologically consistent regions is probably limited by the interplay between topography and climate.

5. Conclusions

In this study, we explored the spatial non-stationarity of the driving mechanism for amphibian species richness. The environmental factors with a higher spatial heterogeneity are more effective in explaining the variation of amphibian diversity. The elevation best explained the variation of species richness in most plateaus as a negative variable, while it became the positive variable in eastern plains. Climatic variables played an important role in maintaining the amphibian diversity, where temperature and precipitation showed high effects and variability. A further increase in temperature exacerbated the suppressive effects of surface solar radiation on amphibians. Anthropogenic impacts significantly increased the sensitivity of amphibian species to environmental changes. Among the identified ecologically consistent regions, the species richness in Yunnan is regulated by integrative multivariate factors and most negatively affected by human activities. These results have important implications for explaining the formation of biodiversity patterns and ecological conservation.

CRediT authorship contribution statement

Zhaoning Wu: Conceptualization, Methodology, Software, Visualization, Formal analysis, Writing – original draft, Writing – review & editing. **Amaël Borzée:** Supervision, Writing – review & editing. **Tianlu Qian:** Validation, Data curation, Visualization. **Wenyu Dai:** Investigation, Software. **Siqing Li:** Investigation, Data curation. **Jiechen Wang:** Supervision, Project administration.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The data that support the findings of this study have been deposited to the Dryad Digital Repository: https://doi.org/10.5061/dryad.j9kd51cgm.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2023.110268.

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